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Acropora in Hawaii. Part 2. Zoogeography[1]

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ABSTRACT: *Acropora* was present in Hawaii during the Miocene but disappeared from the geological record during the Pleistocene. In the present (Holocene), *Acropora* appears to be in the process of recolonizing the archipelago. Three species have been found, all with centers of distribution in the middle of the chain at French Frigate Shoals. The most likely source of the *Acropora* recolonizing Hawaii is Johnston Island by way of the subtropical countercurrent. Few other species of coral in Hawaii were extirpated during the Pleistocene. Thus the history of *Acropora* in the archipelago may not be representative of shallow-water marine forms in general. Nevertheless, the record of *Acropora* in Hawaii supports the theory that distributional discontinuities between many Pacific Island coral reef faunas are due to the net product of local extinction and recolonization.

RECENT RESEARCH in the Northwestern Hawaiian Islands has firmly established the presence of *Acropora* in Hawaii (see Part 1 by Grigg, Wells, and Wallace in this issue). This discovery has resolved over 100 years of controversy in the scientific literature regarding presence of this genus of reef-building coral in Hawaii during recent times. Part 1 reviews the scientific literature concerning *Acropora* in Hawaii, identifies and describes the three species of *Acropora* present in Hawaii, and gives their patterns of distribution and abundance. Ecological aspects of their size–frequency distributions and reproductive behavior are also discussed. This section of the paper (Part 2) considers various hypotheses concerning zoogeographic origins of *Acropora* spp. in Hawaii.

ZOOGEOGRAPHY

Several hypotheses may be advanced to explain the present patterns of distribution and abundance of species of *Acropora* in Hawaii.

1. *Acropora* in Hawaii today may have been introduced by man via vessel traffic between Hawaii and other islands where *Acropora* exists.

2. *Acropora* may have arrived in Hawaii by separation and tectonic rifting of islands from more tropical areas containing *Acropora* populations.

3. *Acropora* may have arrived in Hawaii by way of larval dispersal during the Miocene or earlier. The present distribution may be relict of populations that existed during the Miocene.

4. *Acropora* may be in the process of post-Pleistocene recolonization, primarily by larval dispersal from outside the archipelago. Recolonization may be a process rather than a single event.

Before discussing these hypotheses it is useful first to examine the geological record of *Acropora* in Hawaii as well as the geological history of the Hawaiian Archipelago. Cores on Oahu and Midway islands and dredge hauls off Oahu show that *Acropora* was present at both ends of the archipelago in the Miocene (Menard, Allison, and Durham 1962; Ladd, Tracey, and Gross 1970). *Acropora* disappeared from Hawaii during the late Pleistocene (John W. Wells, personal communication) and is still absent

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at the southeastern and northwestern ends of the chain. Until recently *Acropora* was thought to be absent or extremely rare throughout the archipelago. It is now known that *Acropora* exists on at least six islands in the chain, with the center of distribution at French Frigate Shoals (Part 1). A core 0.4 m in length taken from the reef at a depth of 10 m at French Frigate Shoals provides conclusive evidence that *Acropora* has been on this island for 414 ± 68 years (Part 1)—at least 100 years before Western contact by Captain James Cook in 1778.

The geological history of the archipelago must also be considered before zoogeographic questions of *Acropora* in Hawaii can be discussed. It is now generally accepted that the Hawaiian Archipelago resulted from a series of massive but intermittent extrusions of lava over a melting anomaly or "hot spot" (Wilson 1963, Morgan 1972, Jackson et al. 1980) in the Pacific lithospheric plate. Subsequent drift of the Pacific Plate to the north and northwest has resulted in the successive formation of an almost linear chain of islands. With the exception of Necker Island and Wentworth Seamount, the ages of the islands and seamounts progressively increase moving to the northwest (Jackson et al. 1980). In order to compute the position where each island was formed in the geological past, the rate and direction of drift can be reversed for a period of time equivalent to the age of the islands. This has been done by Rotondo, who has shown that all the islands but two (Necker and Wentworth) were formed at lat. 15° ± 4° N within the last 30 million years (Rotondo 1980, Rotondo et al. in press). Rotondo's analysis indicates that Necker and Wentworth islands were both formed under oceanic conditions more than 70 million years ago at approximately 10° S lat. and 145° W long. Seventy million years ago roughly coincides with the appearance of *Acropora* in the geological record (Moore 1956). The foregoing account describes the historical events against which various possible theories of origin for *Acropora* in Hawaii must be tested.

In light of the geological record, it is unlikely that *Acropora* was introduced to Hawaii by man. We know from the reef core at French Frigate Shoals that *Acropora* was in the Hawaiian Islands at least 100 years before Western contact (see Part 1). There is a remote possibility that *Acropora* could have been introduced by the early Polynesians on the bottoms of their canoes. However, if this were true, *Acropora* should be present in the high islands where the majority of the Hawaiians settled.

The second hypothesis, that *Acropora* in Hawaii was derived from populations that were separated and transported by tectonic processes, is also unsupportable. As described above, it is now generally accepted that the Hawaiian Archipelago originated in an oceanic environment. Colonization in the Miocene or earlier would therefore require larval dispersal as opposed to separation and subsequent drift.

The third hypothesis involves a combination of larval dispersal of *Acropora* to Hawaii during the Miocene or earlier and a pattern of relict survival. Considering the oceanic origin of the archipelago, this hypothesis probably accounts for the distribution of *Acropora* throughout the chain during the Miocene. However, if *Acropora* in Hawaii today is a relict of a population in the past, colonies of the three species should be present in the high islands (Hawaii to Niihau). This presence would be expected for several reasons. First, no other species of coral found in the Hawaiian Archipelago is excluded from the southeastern end (Maragos 1977). Second, water quality at least on offshore reefs is surprisingly similar throughout the chain (Hirota et al. 1980). Third, competitive exclusion would not be expected to affect *Acropora* selectively in the high islands because *Acropora* (due to its high growth and vasiform growth form) appears to be competitively superior to other Hawaiian species of coral at French Frigate Shoals. Fourth, most habitats where *Acropora* is found in the Northwestern Hawaiian Islands (NWHI) are present in the high islands (patch reefs, barrier reefs, offshore reefs, etc.). And fifth, rates of growth, coral cover, and community structure of corals through-

out the archipelago suggest that conditions for coral growth are most favorable at the southeastern end of the chain (Grigg and Dollar 1980) where the most optimal levels of temperature and light are found. Given all of these factors, together with the original dispersal capabilities necessary for colonization; then, if *Acropora* is a relict of the Miocene, it should presently occupy the high islands. Its absence there is a convincing argument against the relict hypothesis.

The fourth hypothesis suggests that the presence of *Acropora* in Hawaii today is due to post-Pleistocene recolonization by larval dispersal. The present-day pattern of distribution and abundance of *Acropora* (see Part 1) could be a result of various combinations of larval recruitment and mortality: either (a) recruitment throughout the archipelago with differential mortality in the southeastern and northwestern ends, (b) larval recruitment in the upper two-thirds of the chain with differential mortality at the northwestern end, or (c) recruitment simply limited to the middle of the chain with no differential mortality.

Differential mortality in the southeastern end of the chain has already been discussed. The evidence available indicates that, if anything, the opposite should be true: the southeastern end of the chain should be more suitable for *Acropora*. Differential mortality at the northwestern end of the chain is also not supported by available evidence. At Laysan, where only two colonies of *A. cytherea* have been found (30,000 m^2 of reef surveyed), both colonies were reasonably large (40 and 95 cm in diameter). Assuming a radial growth of 7 cm/yr (the rate at French Frigate Shoals), the larger colony would be about seven years old. If colonies can survive for this long at Laysan, their absence there is probably due to an absence of recruitment. Hence the present day distribution appears to be entirely the result of a pattern of larval recruitment limited to the central portion of the chain.

Recruitment may depend entirely on sources outside the Hawaiian chain. This is suggested by the immature condition of all colonies of all three species of *Acropora* analyzed over a six-month period (see Table 1, Part 1). If reproduction does occur within the Hawaiian Archipelago, it may be limited to exceptionally warm years and therefore would be very sporadic. If this suggestion is correct, the present patterns of distribution and abundance of the three species should reflect the position and strength of a current responsible for larval transport. The accumulating data on the subtropical countercurrent provide strong support for this argument and point to Johnston Island as the likely source of *Acropora* larvae. All three species of *Acropora* in Hawaii occur at Johnston Island.

Physical Oceanography

The dominant current system in the Hawaiian Archipelago is the North Pacific Equatorial Current (NPEC) (Sverdrup, Johnson, and Fleming 1942). The NPEC flows from east to west generally at speeds less than 20 cm/sec. Until recently, the existence of a countercurrent running west to east was unknown in this region. On the basis of bathythermograph data, Margaret Robinson (1969) predicted that such a current should exist between lat. 22° N and 25° N (Figure 1), and extend from the western boundary of the Pacific to the region of the Hawaiian Islands. She called the current the Subtropical Countercurrent (SCC). More detailed studies by Hasunuma and Yoshida (1978) have shown that the SCC consists of a train of anticyclonic eddies about 300–600 km across (mesoscale phenomena), which break off from the Kuroshio and head east at about lat. 20° N, with variable speed but occasionally accelerating to over 50 cm/sec. Hasunuma's data confirm that the SCC extends all the way to the Hawaiian Archipelago.

The presence of a northeasterly flow in the central region of the archipelago was first detected by Seckel in 1962, but at that time it was not recognized as a countercurrent (Seckel 1962). Seckel's charts of both sea surface temperature (Figure 2) and dynamic topography of the surface show that intrusions of northeasterly flowing water occur

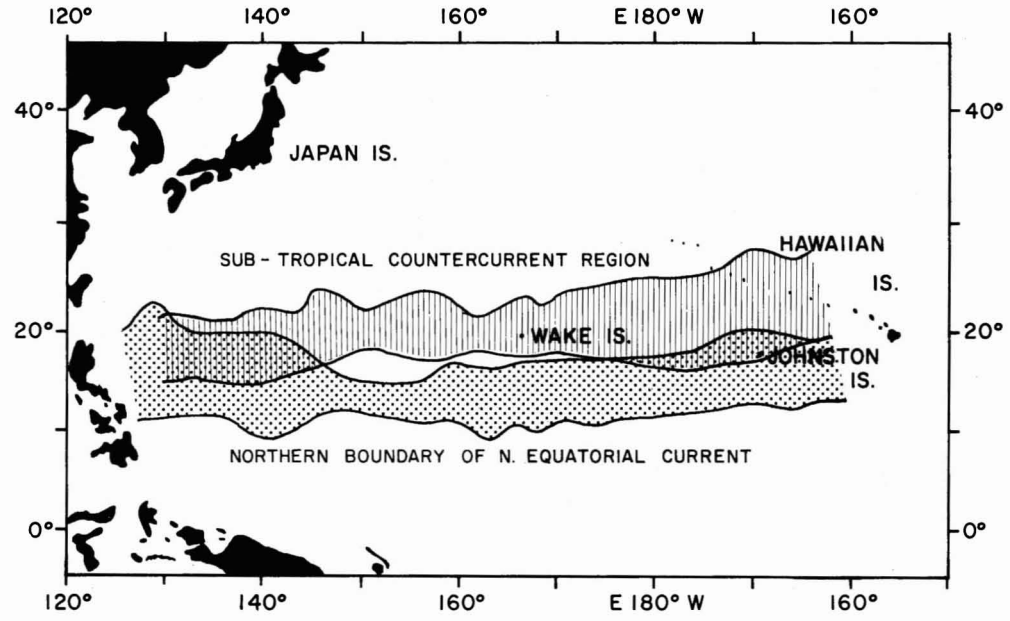

FIGURE 1. Geographic location of the Subtropical Countercurrent and the North Equatorial Current in the western Pacific Ocean (from Robinson 1969).

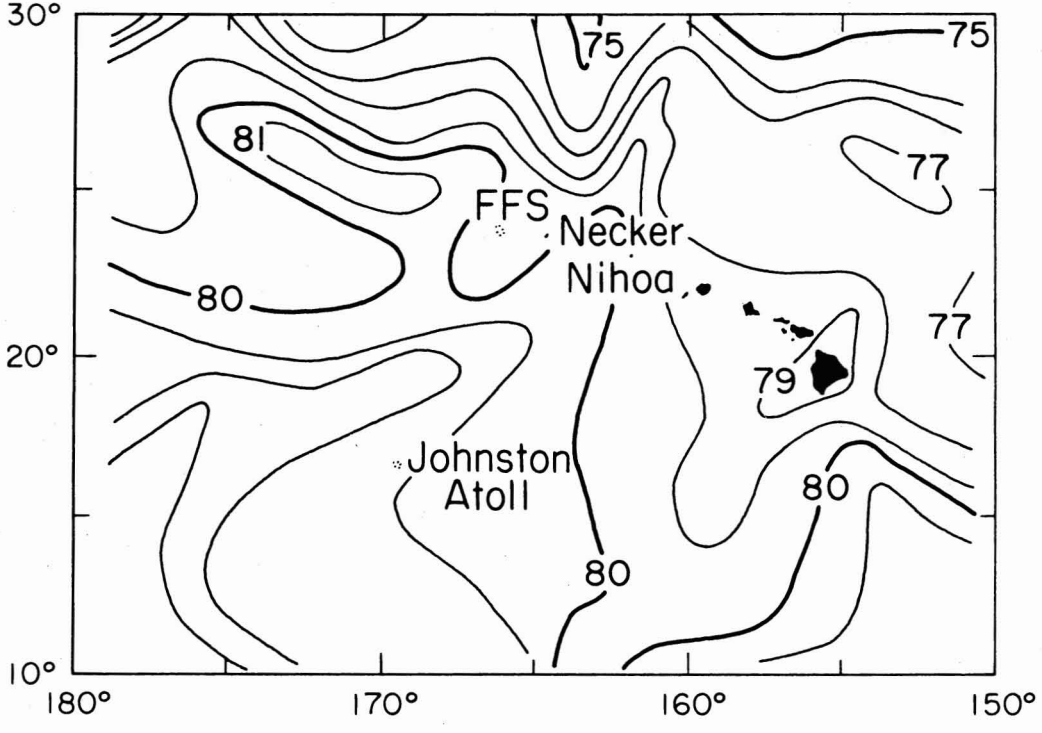

FIGURE 2. Displacement of sea surface isotherms to the northeast in the region of Necker Island in the month of October may be caused by advection from the Subtropical Countercurrent (from Seckel 1962).

intermittently, especially during the summer and fall months, near Nihoa, Necker, and French Frigate Shoals.

The only published direct measures of currents in the Northwestern Hawaiian Islands are those by Patzert, Wyrtki, and Santamore (1970), made during April, May, and June, 1969. They placed current meters 10 m below the surface on the shallow shelves of nine islands in the NWHI. The 45-day records all show a general flow to the north, with the strongest mean flow at French Frigate Shoals (6.6 cm/sec) and Nihoa (6.2 cm/sec) (Figure 3). It is likely that this flow represents the northwestern extremity of the Subtropical Countercurrent (K. Wyrtki, personal communication). Unpublished records of satellite tracked drift buoys deployed during the NORPAX program in 1979 and 1980 also show a sharp deflection to the northeast in the area between Johnston Island and French Frigate Shoals (W. C. Patzert, personal communication). The cause of the deflection is unknown but it could be due to the buoys crossing northward from the NPEC to the SCC.

Research on currents in the high islands (Hawaii to Niihau) shows no such consistent flow to the northeast (Wyrtki, Graefe, and Patzert 1969). During the period 1965–1969, Wyrtki and his coworkers placed 43 current meters around the high islands and found that flow was variable, rather independent of local winds, and generally inconsistent from place to place. These observations and data suggest that the Subtropical Countercurrent does intersect the Hawaiian Archipelago, but only at longitudes west of the major high islands, and could provide the means of *Acropora*'s dispersal to the central Hawaiian Islands from Johnston Island or even possibly Wake Island (Figure 1).

Coral Larval Behavior

Successful larval recruitment from Johnston or some other island requires that transport time not exceed the maximum limits of larval life. The distance from French Frigate Shoals, the center of the distribution of *Acropora* in Hawaii, to Johnston Island is 720 km; the distance to Wake Island is 2700 km. The velocity of the Subtropical Countercurrent in the region of the Hawaiian Archipelago is not well documented. Patzert (1973) found that the mean resultant drift toward the northeast at French Frigate Shoals was 6.6 cm/sec. However, short-term intermittent measures greatly exceeded this value. Wyrtki (1973) has shown that the equatorial countercurrent may vary by 2.5 times the mean for periods up to several months. If a factor of 2.5 is applied to Patzert's mean of 6.6 cm/sec, the value produced would be 16.5 cm/sec. If this figure is taken as an estimate of maximum flow, the travel time from Johnston Island to French Frigate Shoals would be 50 days; from Wake Island, 187 days.

Both of these timespans exceed the larval lives of most species of reef-building corals, but the 50-day value does not exceed the upper limits of that range by much. Generally, coral larvae settle within three or four weeks (Atoda 1951, Harrigan 1972, Rinkevich and Loya 1979). However, many are capable of postponing settlement for longer periods. Rinkevich and Loya (1979) found the maximum survival time of *Stylophora pistillata* to be 35 days. Atoda (1951) similarly found the maximum survival time for the larvae of *Galaxea aspera* to be 49 days. Other studies have shown that some coral larvae can be maintained in the laboratory without settling for much longer periods. Gorgonian larvae have been kept for 73 days (Grigg 1979) and *Pocillopora damicornis* larvae have been kept for 212 days (Harrigan 1972). In addition to the possibility of a prolonged larval life as a means of bridging the gap between Johnston Island and the central Hawaiian Islands, it is also possible that larval settlement on flotsam could occasionally occur. In either case, it would appear that the most likely source of colonization of *Acropora* in Hawaii is Johnston Island by way of the Subtropical Countercurrent.

CONCLUSIONS

Several independent lines of evidence suggest that the present patterns of distribution

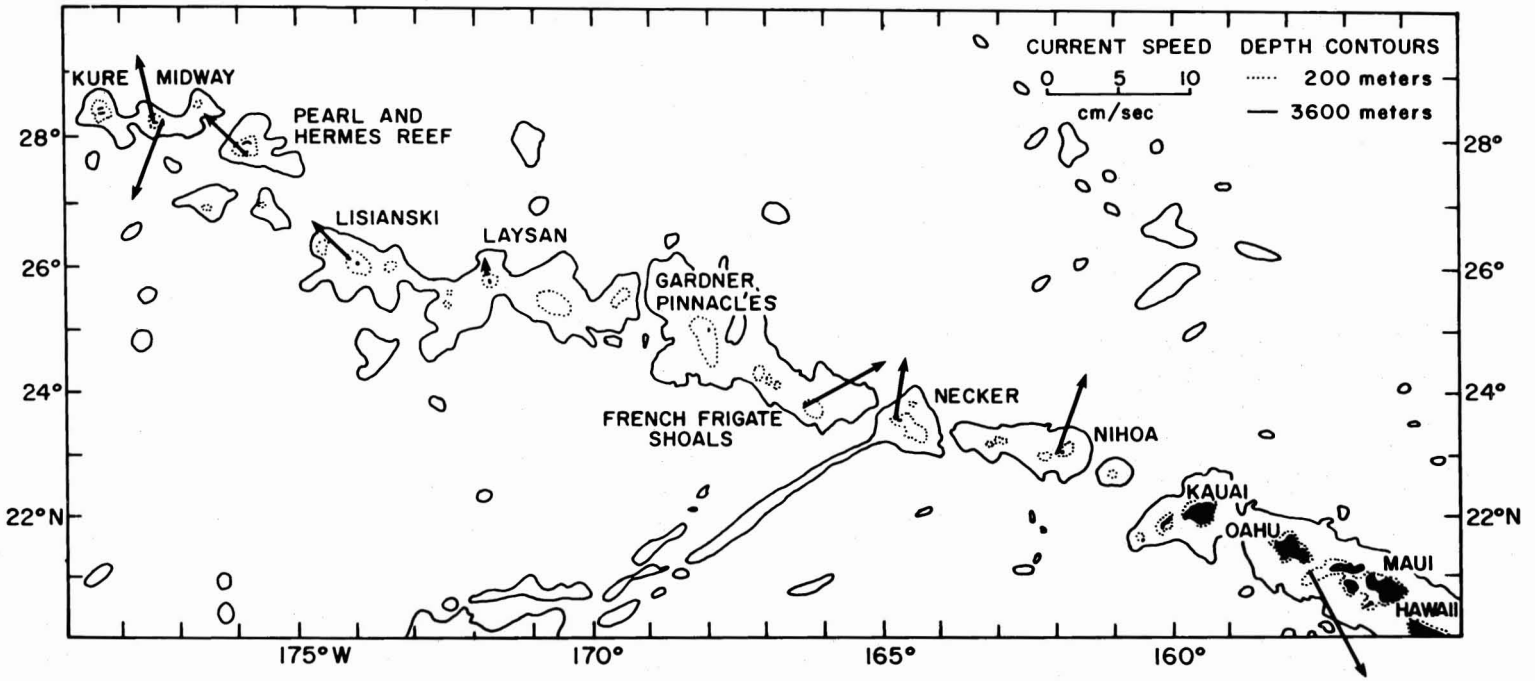

FIGURE 3. Resultant drift calculated from eight simultaneous near-surface current measurements made with moored current meters in the Hawaiian Archipelago in April–May of 1969 (from Patzert 1973).

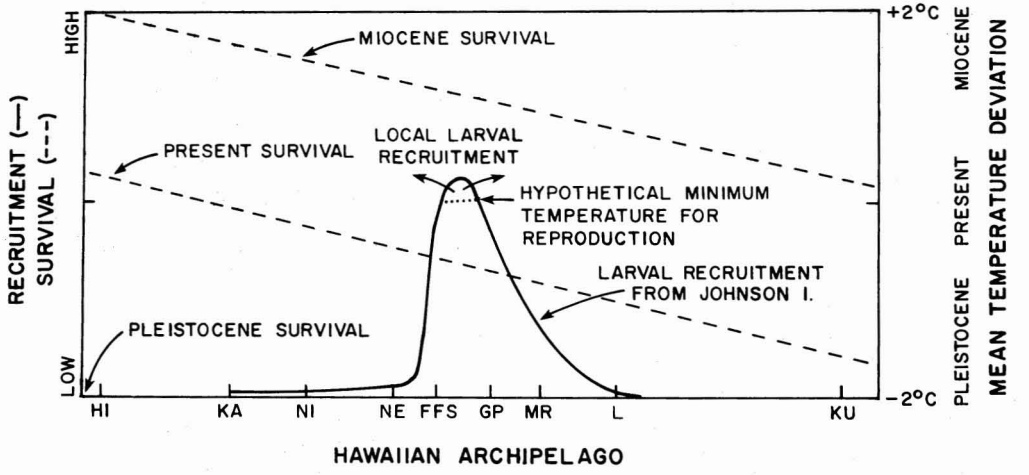

FIGURE 4. Hypothetical model showing the effect of environment on the present and past distribution (recruitment, survival, and reproduction) of *Acropora* in Hawaii. The slope of the survival curve in the present, Miocene, and Pleistocene is based on the relationship between growth rate of *Porites lobates* and latitude (Grigg and Dollar 1980). In the Miocene, temperature was higher and reproduction within the archipelago led to rapid colonization of all islands. During the glacial recession of the Pleistocene, survival went to zero and *Acropora* became extinct in the Hawaiian Archipelago. At the present, the center of distribution is French Frigate Shoals. *Acropora* is in the process of recolonizing the archipelago. Reproduction locally may or may not occur. The distribution is maintained primarily by recruitment from Johnston Island. At the southern end of the archipelago, conditions are suitable but there is no recruitment. The high islands are too far from Johnston Island and currents are unfavorable. Interisland recruitment is minimal or absent. At the northwestern end of the chain beyond Laysan Island, *Acropora* is absent because there is no recruitment. Mean temperature deviations during the Pleistocene and Miocene are based on data from Savin (1977) and McIntyre et al. (1976). HI = Hawaii, KA = Kauai, NI = Nihoa, NE = Necker, FFS = French Frigate Shoals, GP = Gardner Pinnacles, MR = Maro Reef, L = Laysan Island, KU = Kure Atoll.

and abundance of all three species of *Acropora* in Hawaii are due primarily to recruitment outside the archipelago, probably from Johnston Island. Analyses of the reproductive condition of large colonies of *Acropora* at French Frigate Shoals, Maro Reef, and Laysan Island show all material to be immature (Part 1). If reproduction does occur within the archipelago, it is probably very sporadic and limited to French Frigate Shoals. This would result in occasional pulses of larvae reaching nearby islands, such as Gardner Pinnacles. But, if reproduction were occurring with any frequency at French Frigate Shoals or other islands within the chain, *Acropora* would be expected to be more widespread in the Hawaiian Archipelago than it is. The widest channel is 185 km and most are only about 100 km. Perhaps the best evidence that *Acropora* in Hawaii are expatriates, maintained primarily by outside recruitment, is the close fit between the patterns of distribution and abundance, on the one hand, and the strength and position of the Subtropical Countercurrent where it intersects the Hawaiian Archipelago, on the other. The SCC has been shown to be intermittent and vary in position where it intersects the Hawaiian chain (Seckel 1962, Robinson 1969, Patzert 1973) but it appears rarely if ever to reach as far southeast as the main Hawaiian Islands (Wyrtki, Graefe, and Patzert 1969) or as far northwest as Lisianski, Pearl and Hermes, Midway, and Kure (Patzert 1973).

In conclusion, *Acropora* was present throughout the Archipelago during the Miocene but appears to have disappeared during the Pleistocene and is presently in the process of recolonization. The route of recolonization appears to be from Johnston Island by way of the Subtropical Countercurrent. A model which summarizes the net effect of recruitment, survival, and reproductive behavior of *Acropora* in the present and the past is presented in Figure 4.

The colonization route apparently taken by *Acropora* to Hawaii almost certainly does not apply generally to other components of the marine biota in Hawaii. The only other species for which the *Acropora* pattern specifically applies is the striated butterflyfish, *Chaetodon* (*Megaprotodon*) *trifascialis*, which is an obligate coralivore that feeds exclusively on *Acropora cytherea*. *C. trifascialis* is also known from Johnston Atoll. Other routes of colonization are illustrated by the fishes *Oplegnathus punctatus* and *O. fasciatus* (Hobson 1980), which show strong faunal ties with Japan and probably arrived in Hawaii by way of the North Pacific Drift, an extension of the Kuroshio Current. The southern extension of the Kuroshio has also been labeled (by Zinsmeister and Emerson 1979) as a western source for the marine molluscan fauna of Hawaii. However, Zinsmeister and Emerson do not acknowledge the existence of the Subtropical Countercurrent. They speculate that the molluscan fauna of Johnston Atoll is a Hawaiian derivative, rather than vice versa as suggested by Kay (1967), Amerson and Shelton (1976), and in the present paper. It is of course possible that transport between the Hawaiian Archipelago and Johnston Atoll is bidirectional, since Johnston Atoll lies near the boundary of the eastward flowing SCC and the westward flowing NPEC (Figure 1). Another possible route to Hawaii is from the southeast by island integration in connection with northwestward drift of the Pacific lithospheric plate (Rotondo et al. in press).

EVOLUTIONARY SIGNIFICANCE

Several other genera of Miocene corals known from the fossil record in Hawaii (*Platygyra*, Menard, Allison, and Durham 1962; *Stylophora* and *Seriatopora*, John W. Wells, personal communication) disappeared at the end of the Miocene and apparently have not recolonized the chain. Moreover, the proposed pattern of extirpation and recolonization of *Acropora* in Hawaii is not typical of most other corals in Hawaii, which have continuous distributions throughout the archipelago (Grigg and Dollar 1980). Hence, the faunal decimation which may have affected *Acropora* appears to have been very selective. The high degree of endemism now found in Hawaii for such species groups as marine fishes (29 percent, Randall 1976) also suggests that many species survived the Pleistocene glaciations. Even so, the record of *Acropora* in Hawaii provides strong evidence that Hawaiian reefs were partially defaunated during the Pleistocene, and supports the theory that distributional discontinuities among the faunas of many Pacific Island coral reefs are due to the net product of local extinction and recolonization, as suggested by Maragos and Jokiel (1978) and predicted theoretically by MacArthur and Wilson (1967).

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